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Feedback control for competition models with different removal rates in the chemostat

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Abstract: We consider the feedback control for a model of competition in a chemostat with one single substrate and two species. De Leenheer and Smith [*J.Math.Biol.*,46 (2003), pp.48-70] studied the competition in the chemostat in the framework of feedback control theory, giving sufficient conditions for the convergence of the species toward a unique stable critical point, thus avoiding the competitive exclusion. Nevertheless, they suppose that the mortality rates can be neglected. In this paper we allow non–zero mortality rates and the results stated before can be extended: We also obtain sufficient conditions (summarized as upper bounds for the size of mortality rates) for the convergence of competing species toward a unique stable critical point.

Key-words: Chemostat, Competition model, Feedback control, Competitive dynamical systems, Global asymptotic stability

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Commande en boucle fermée pour un modèle de compétition dans un chemostat avec différentes taux de dilution

Résumé : Dans cet article, nous considérons un problème de commande d'un modèle de compétition dans le chemostat avec un substrat et deux espèces. De Leenheer et Smith [*J.Math.Biol.*,46 (2003),pp.48–70] ont etudié la compétition dans le chemostat depuis une perspective fournie par la théorie du contrôle; et obtiennent des conditions suffisantes pour la convergence des espèces vers un point d'équilibre stable, et en conséquence evitant l'exclusion compétitive. Neanmoins, ils supposent qui les taux de mortalité peuvent être negligées. Dans cette article nous permettons des taux de mortalité non–négatives et les résultats précédents peuvent être généralisés: Nous obtenons des conditions suffisantes (resumés comme des bornes supérieures pour le taux de mortalité) pour la convergence des espèces en compétition vers un unique point d'équilibre stable.

Mots-clés : Chemostat, Modèle de compétition, Commande en boucle fermée, Système dynamique compétitif, Stabilité asymptotique globale

1 Introduction

A chemostat is a continuous culture device in which microorganisms grow, submitted to a flow of nutrients. It can be used to study microbial physiology and metabolism, for modeling the wastewater treatment process, the biological waste decomposition or the competition between different species of microorganisms for a single substrate. Models of chemostat have been extensively studied mathematically (for a complete background we refer the reader to [19]), mainly with ordinary differential equations.

The competition in the chemostat with a single substrate and two species of microorganisms has been studied by several authors and the generic asymptotic behavior predicted by the theory is the *competitive exclusion principle* (see *e.g.* [1],[2],[8],[9],[12],[15],[19],[24]), which means –roughly speaking– that at most one competing species avoids extinction.

Several ways to circumvent the competitive exclusion principle have been proposed; in this paper we focus our attention on control theory and its applications to chemostat models. By considering some parameters of chemostat (for example input flow nutrient, input nutrient concentration and/or others) as control variables, a family of control laws allowing the coexistence between the species has been constructed. In [4],[13],[16],[18],[25] some of these parameters have been taken as positive functions of time (open–loop control) and the coexistence between the species is obtained in the form of periodic functions, quasi–periodic functions and more general positive functions of time.

On the other hand, De Leenheer and Smith [5] built a family of feedback control laws (closed–loop control) for the model described above using the dilution rate (input flow nutrient) as the control variable. They prove the global asymptotic stability of the closed–loop model toward an interior critical point, making possible the coexistence between the two species. The underlying hypotheses of their model are the monotony of uptake functions and the assumption that the specific mortality rates of species are negligible in comparison with the dilution rate and hence can be ignored.

In the present work, our goal is to extend the results given in [5] dropping the assumption $d_i = 0$. We point out that the assumption $d_i > 0$ implies that asymptotically in time, none of the equations can be eliminated as in the case $d_i = 0$ and consequently, monotone dynamical systems theory cannot be applied directly to study the asymptotic behavior of chemostat model. Nevertheless, if we suppose that the mortality rates have suitable boundedness properties. We will be able to present a set of verifiable conditions that ensure the global asymptotic stability of a unique critical point in the positive orthant; we focus our attention on the upper bound of mortality rates.

We show that when the mortality rates are relatively small, the asymptotic behavior of the closed–loop system is the convergence to an interior critical point. In fact, we show that the asymptotic behavior of the closed–loop model can be deduced from the study of a set of low-dimensional (planar) differential equations and using differential inequalities. This will be useful in proving that there exists a globally attractive compact set K^*; finally we will build a Lyapunov-like function defined in K^*, proving the global asymptotic stability of a critical point in K^*.

This paper is organized as follows. In Section 2 we have compiled some facts concerning the competition chemostat model with two species and without control. In Section 3 we provide an exposition of the feedback control law, state some hypothesis related to mortality rates and expose the main result of coexistence. Section 4 presents some preliminary results related to asymptotic behavior of the model with control. The proof of the main result is given in Section 5.

2 Model of competition in the chemostat

The chemostat model with competition is described by the following equations (see [19, Chapt.1] for a more complete discussion of the model):

$$\left\{\begin{array}{l} \dot{s} \;\; = D(s_{in}-s) - \frac{x_1}{y_1}f_1(s) - \frac{x_2}{y_2}f_2(s), \\ \dot{x}_1 = x_1(f_1(s) - D - d_1), \\ \dot{x}_2 = x_2(f_2(s) - D - d_2). \end{array}\right. \tag{1}$$

In model (1), s denotes the concentration of the substrate in the chemostat at time t, x_i denotes the biomass density of the ith species at time t, $f_i(s)$ represents the per-capita growth rate of nutrient of the ith population and so y_i is a growth yield constant; D and s_{in} denote, respectively, the dilution rate of the chemostat and the concentration of the input substrate. Finally d_i denotes the death rate of the ith species.

Throughout this paper, we assume that $f_i\colon \mathbb{R}_+ \mapsto \mathbb{R}_+$ (for $i=1,2$) satisfies the following properties **(F)**:

(F1) f_i is continuously differentiable, monotone increasing and $f_i(0)=0$.

(F2) There exists one root $u^* \in (0, s_{in})$ of $f_1(s) - f_2(s) = 0$. Moreover:

$$\left\{\begin{array}{lll} f_1(s) > f_2(s) & \text{if} & s \in (0, u^*), \\ f_1(s) < f_2(s) & \text{if} & s \in (u^*, +\infty). \end{array}\right.$$

(F3) The equation:

$$f_1(s) - f_2(s) - d_1 + d_2 = 0 \quad s \in (0, s_{in}) \tag{2}$$

has two roots w^* and s^* ($w^* < s^* < u^*$) when $d_1 > d_2$ and has one root $s^* \in (u^*, s_{in})$ when $d_1 \leq d_2$.

(F4) There exists a constant $\varepsilon_0 \in (0, s^*/2)$ such that $\hat{s}(\alpha,\beta) \in V_{\varepsilon_0} = (s^* - \varepsilon_0, s^* + \varepsilon_0)$ is a root of the equation:

$$f_1(s-\alpha) - f_2(s-\beta) - d_1 + d_2 = 0 \quad \text{with} \quad \alpha,\beta \in [0,k_0] \subset [0,\varepsilon_0). \tag{3}$$

Moreover, if Eq.(3) has another solution, it must be in $(\max\{\alpha,\beta\}, \max\{\alpha,\beta\}+\varepsilon_0)$.

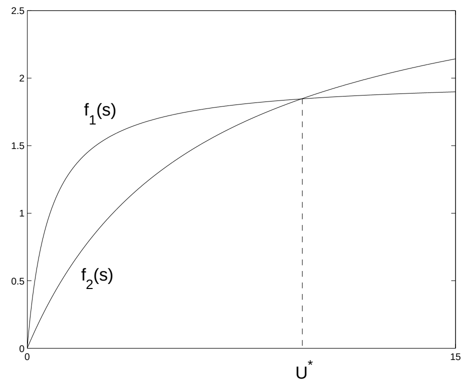

Figure 1: Geometric interpretation of **(F2)**: Graph of f_1 and f_2

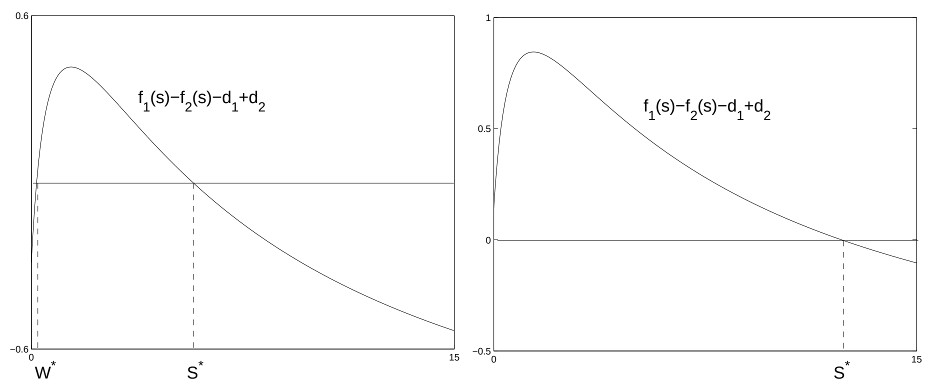

Figure 2: Geometric interpretation of **(F3)**: Graph of the function $f_1 - f_2 - d_1 + d_2$, with $d_1 > d_2$ (Left) and $d_1 \leq d_2$ (Right)

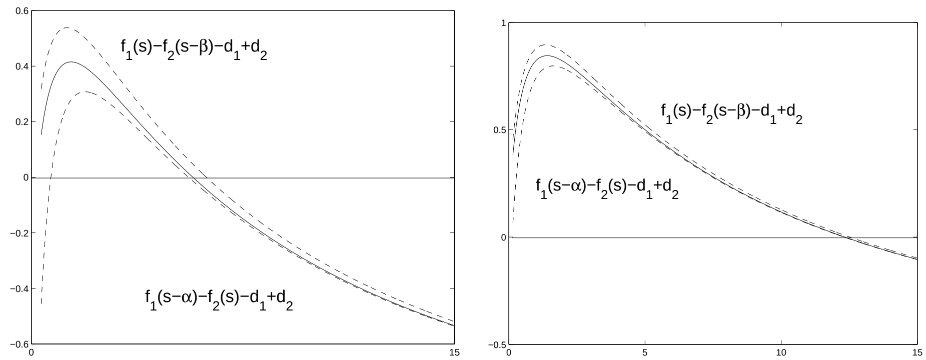

Figure 3: Geometric interpretation of **(F4)**: The dashed graphs are the *worst perturbations* possible to Eq.(2), with $d_1 > d_2$ (Left) and $d_1 \leq d_2$ (Right)

Properties **(F1)**–**(F4)** deserve some comments: **(F1)**–**(F2)** can be considered as "generic properties" of competition chemostat models. Otherwise, **(F3)**-**(F4)** can be viewed as "small perturbations" of **(F2)** and suppose implicitly that mortality rates d_i are relatively small with respect to the parameters of functions f_i.

Property **(F1)** is verified by the functions Holling type I,II and III which are widely used in theoretical ecology (see for example [14, Chapt.5]). Moreover, in several experiments it has been observed that the Michaelis-Menten function:

$$f_i(s) = \frac{\mu_i s}{s + k_i}, \quad \mu_i, k_i > 0$$

so called also Monod function (a class of Holling type II function) provides a reasonable approximation for the experimental data (see for example [8],[19]).

Property **(F2)** is usual in competition theory of chemostat; as it has been pointed out in [19, p.24], in the special case $d_i = 0$ $(i = 1, 2)$ and $D = f_1(u^*) = f_2(u^*)$, assumption **(F2)** implies that there exists a positively invariant and globally attractive set:

$$\Sigma = \left\{ (s, x_1, x_2) \in \mathbb{R}^3_+ : \frac{x_1}{y_1} + \frac{x_2}{y_2} = s_{in} - u^* \quad \text{and} \quad s = u^* \right\}$$

Property **(F3)** is verified if and only if one of the following (see Fig.2) inequalities is verified:

$$0 < d_1 - d_2 < \max_{s \in (0, u^*)} f_1(s) - f_2(s),$$

$$0 \geq d_1 - d_2 > \min_{s \in (u^*, s_{in})} f_1(s) - f_2(s);$$

Property **(F4)** is a straightforward consequence of **(F2)** and **(F3)**: Notice that the functions $f_1(s) - f_2(s) - d_1 + d_2$ and $f_1(s - \alpha) - f_2(s - \beta) - d_1 + d_2$ have the same asymptotic behavior and their graphs present differences only in a neighborhood of $\max\{\alpha,\beta\}$ (see Fig.3).

Moreover, if $\alpha=\beta=0$ Eq.(3) is equivalent to Eq.(2), hence **(F3)** gives the existence of a solution $\hat{s}(0,0)=s^*$. Finally, implicit function theorem implies the existence of a number ε_0 such that Eq.(3) has a solution in a neighborhood V_{ε_0} of s^*. A careful observation of the implicit function theorem reveals that upper bounds for ε_0 can be estimated.

In summary, this properties are easily verified by a couple of functions f_1 and f_2 provided that d_i and ε_0 are relatively small with upper bounds to be defined later in the text.

2.1 Competitive exclusion principle and Persistence

It is well known that the asymptotic behavior of system (1) is the *competitive exclusion principle*; the main features of this one are shown in [12], [19], [24] (theoretical results) and [8] (experimental results) and are recalled by the following result tailored for $n=2$ and increasing functions f_i:

Proposition 1 (Competitive exclusion principle [12],[24]) *Suppose that the properties* **(F1)**–**(F2)** *are verified and the equations $f_i(s)=D+d_i$ have one solution $\lambda_i\in(0,s_{in})$. Let us build the functions $h_{i,j}\colon(0,\lambda_i)\cup(\lambda_j,s_{in})\mapsto\mathbb{R}$ defined for any $i,j\in\{1,2\}$ by :*

$$h_{i,j}(s)=\frac{[f_i(s)-D-d_i](s_{in}-\lambda_i)f_j(s)}{D[f_j(s)-D-d_j](s_{in}-s)}.$$

(i) If $\lambda_1<\lambda_2$ and $\max\limits_{s\in(0,\lambda_1)}h_{1,2}(s)\leq\min\limits_{s\in(\lambda_2,s_{in})}h_{1,2}(s)$ then all solutions of Eq.(1) with $x_1(0)>0$ satisfy:

$$\lim_{t\to+\infty}(s(t),x_1(t),x_2(t))=(\lambda_1,y_1D(s_{in}-\lambda_1)/(D+d_1),0).$$

(ii) If $\lambda_2<\lambda_1$ and $\max\limits_{s\in(0,\lambda_2)}h_{2,1}(s)\leq\min\limits_{s\in(\lambda_1,s_{in})}h_{2,1}(s)$ then all solutions of Eq.(1) with $x_2(0)>0$ satisfy:

$$\lim_{t\to+\infty}(s(t),x_1(t),x_2(t))=(\lambda_2,0,y_2D(s_{in}-\lambda_2)/(D+d_2)).$$

That means, at most one competitor population avoids extinction.

As in [5], we see the chemostat as a feedback control system; that means a system with three components: A *plant* (the chemostat to be controlled), a *sensor* to measure the output $y(t)$ of the plant, and a *controller* to generate the plant input. Our goal is to build a feedback control law for the system (1) that render the closed–loop system coexistent (also called *permanent* [11] or *uniformly persistent* [19, Appendix D]), and additionally establish existence of an interior point globally asymptotically stable.

3 Statement of the problem and main result

3.1 Statement of the control framework

We need to define the control variables, *i.e.* the inputs and the online available variables, *i.e.* the outputs. In the chemostat model, the control variables usually employed are the dilution rate D and/or the input nutrient concentration s_{in}. In this work we will suppose that s_{in} is fixed and D will be the only control variable.

The outputs usually considered in chemostat models are functions $y\colon \mathbb{R}^3 \mapsto \mathbb{R}^k$ $(k \leq 3)$ of variables s and x_i. We will suppose in this paper that $k = 1$ and $y = x_1 + x_2$, because, in several cases, technical difficulties do not allow to measure x_1 and x_2 independently and it is necessary to consider total biomass. For example, the measurement is done often by photometric methods (see for example [17],[22] and the references given there) that do not allow to distinguish between the two species.

Hypothesis 1 *Input/Output assumptions are summarized as follows:*
- *The dilution rate D is the feedback control variable of system* (1).
- *$y = x_1 + x_2$ is the only output available of system* (1).

We define the feedback control law $D : \mathbb{R}_+^2 \mapsto \mathbb{R}_+$ by:

$$D(x_1, x_2) = g(x_1 + x_2). \tag{4}$$

Where $g : \mathbb{R}_+ \mapsto \mathbb{R}_+$ is a continuously differentiable, increasing and locally Lipschitz function. Moreover we suppose the following properties **(G)** on the control law g:

(G1) The value $g(0)$ has the restrictions:

$$f_i(\varepsilon_0) < g(0) < f_i(s^* - \varepsilon_0) - d_i \quad \text{for all } i = 1, 2. \tag{5}$$

(G2) For any α,$\beta \in [0, k_0)$ the numbers $\hat{s}(\alpha, \beta) \in V_{\varepsilon_0}$ defined in **(F4)** verify:

$$g(y_{\max}[s_{in} - \hat{s}(\alpha, \beta)]) > f_1(\hat{s}(\alpha, \beta) - \alpha) - d_1 > g(y_{\min}[s_{in} - \hat{s}(\alpha, \beta)]), \tag{6}$$

$$g(y_{\max}[s_{in} - \hat{s}(\alpha, \beta)]) > f_2(\hat{s}(\alpha, \beta) - \beta) - d_2 > g(y_{\min}[s_{in} - \hat{s}(\alpha, \beta)]). \tag{7}$$

It is of interest to identify classes of functions g where properties **(G1)**–**(G2)** can always be found, and hence our control law applied. **(G1)** is always easy to verify. Notice that Eqs.(6)–(7) are always verified when $\alpha = \beta = 0$ (see Fig.4), so by continuity of functions g and f_i it is possible to find a family of functions g satisfying **(G1)**–**(G2)** for a relatively small value of k_0.

Replacing D by the feedback control law (4), system (1) becomes:

$$\begin{cases} \dot{s} &= g(x_1 + x_2)(s_{in} - s) - \dfrac{x_1}{y_1} f_1(s) - \dfrac{x_2}{y_2} f_2(s), \\ \dot{x}_1 &= x_1(f_1(s) - g(x_1 + x_2) - d_1), \\ \dot{x}_2 &= x_2(f_2(s) - g(x_1 + x_2) - d_2). \end{cases} \tag{8}$$

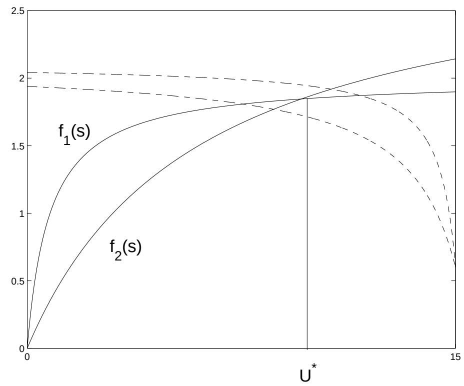

Figure 4: Geometric interpretation of Eqs.6 and 7 when $\alpha = \beta = 0$ (and consequently $\hat{s}(0,0) = u^*$)

The case $d_1 = d_2 = 0$ has been studied by De Leenheer and Smith [5, Th.2]. We summarize their main result (using a slightly different notation):

Proposition 2 (De Leenheer and Smith,[5]) *The system* (1) *with properties* **(F1)**–**(F2)**, *the output* $y = (x_1\ x_2)^T$ *and the control function*:

$$g(x_1, x_2) = \frac{k_1}{y_1} x_1 + \frac{k_2}{y_2} x_2 + \varepsilon \quad \text{with } k_1 > k_2 > 0 \text{ and } 0 \le \varepsilon < f_1(s_{in})$$

has an interior critical point (u^*, e_1^*, e_2^*) *globally asymptotically stable. The constants* e_i^* *are defined by*:

$$e_1^* = \frac{y_1[s_{in} f_1(u^*) - k_2(s_{in} - u^*)]}{k_1 - k_2}, \quad e_2^* = \frac{y_2[k_1(s_{in} - u^*) - s_{in} f_2(u^*)]}{k_1 - k_2}.$$

Remark 1 (a) *Although in [5] it is supposed explicitly that* $y = (x_1\ x_2)^T$, *this assumption can be dropped by using an output* $y = x_1 + x_2$ *and the result above is still valid whenever* $y_1 > y_2$.
(b) *Taking* $y = x_1 + x_2$ *and supposing* $y_1 > y_2$, *the authors extend this result in [7] considering more general uptake functions.*

The assumption $d_i > 0$ makes the study of system (8) far more complex than the case $d_i = 0$; indeed under assumptions $d_i = 0$ the asymptotic behavior of system (8) can be analyzed by studying a reduced planar system. However, this assumption could be questionable because it would limit the use of the model to systems with relatively high dilution rates.

3.2 Main Result: Global asymptotic stability of a critical point

This subsection is devoted to the statement of our main result; this one ensures sufficient conditions for the global asymptotic stability of the critical point (s^*, x_1^*, x_2^*) of system (8), where g^{-1} is the inverse function of g, s^* is the root of Eq.(2) and x_1^*,x_2^* are defined by:

$$x_1^* = \frac{y_1\{y_2[f_1(s^*) - d_1](s_{in} - s^*) - f_2(s^*)g^{-1}(f_1(s^*) - d_1)\}}{f_1(s^*)y_2 - f_2(s^*)y_1},$$

$$x_2^* = \frac{y_2\{f_1(s^*)g^{-1}(f_1(s^*) - d_1) - y_1[f_1(s^*) - d_1](s_{in} - s^*)\}}{f_1(s^*)y_2 - f_2(s^*)y_1}.$$

Let us now introduce some notation and make precise the mathematical setting: we will work with the roots $\hat{s}(\alpha,\beta)$ of Eq.(3) and denote $\hat{s}(\alpha,\beta) = \hat{u}(\alpha,\beta)$ when $\alpha > \beta$ and $\hat{s}(\alpha,\beta) = \hat{v}(\alpha,\beta)$ when $\alpha \le \beta$.

Let $\hat{u}_0$ and $\hat{v}_0$ be the solutions of Eq.(3) with $(\alpha,\beta) = (k_0, 0)$ and $(\alpha,\beta) = (0, k_0)$ respectively. We shall build two sequences $\{m_j\}_j$,$\{M_j\}_j$ of nonnegative terms upperly bounded by ε_0 as we will see later on the proof. We suppose that $m_0 = -k_0$ and $M_0 = 0$; the terms for any integer $j \ge 1$ are defined recursively by:

$$m_j = \frac{\left[\frac{d_1}{y_1}v^*_{1_{j-1}} + \frac{d_2}{y_2}u^*_{2_{j-1}}\right]}{g(u^*_{1_{j-1}} + v^*_{2_{j-1}})} \quad \text{and} \quad M_j = \frac{\left[\frac{d_1}{y_1}u^*_{1_{j-1}} + \frac{d_2}{y_2}v^*_{2_{j-1}}\right]}{g(v^*_{1_{j-1}} + u^*_{2_{j-1}})}. \tag{9}$$

Moreover, the numbers $u^*_{1_j}$,$u^*_{2_j}$,$v^*_{1_j}$ and $v^*_{2_j}$ $(j = 1, 2, \ldots)$ are defined by:

$$\begin{cases} u^*_{1_j} &= \frac{y_1\left\{y_2[s_{in} - \hat{u}_j] - g^{-1}(f_2(\hat{u}_j - m_j) - d_2)\right\}}{y_2 - y_1}, \\ u^*_{2_j} &= \frac{y_2\left\{g^{-1}(f_2(\hat{u}_j - m_j) - d_2) - y_1[s_{in} - \hat{u}_j]\right\}}{y_2 - y_1}, \\ v^*_{1_j} &= \frac{y_1\left\{y_2[s_{in} - \hat{v}_j] - g^{-1}(f_1(\hat{v}_j - M_j) - d_1)\right\}}{y_2 - y_1}, \\ v^*_{2_j} &= \frac{y_2\left\{g^{-1}(f_1(\hat{v}_j - M_j) - d_1) - y_1[s_{in} - \hat{v}_j]\right\}}{y_2 - y_1}. \end{cases} \tag{10}$$

The constants $\hat{u}_j$ and $\hat{v}_j$ $(j = 1, 2, \ldots)$ are the solutions of Eq.(3) with $(\alpha,\beta) = (m_j, M_j)$ and $(\alpha,\beta) = (M_j, m_j)$ respectively.

We are now in a position to state our main result:

Theorem 1 (Main Result) *Suppose that* $y_{\max} = y_1$ *and properties* **(F)** and **(G)** *are verified. If there exists an integer* $j \in \{1, 2, \ldots\}$ *such that the following inequalities hold:*

$$d_i < \frac{\varepsilon_0 g(0)}{2s_{in}}, \tag{11}$$

$$d_i < \frac{M_j f_i(s_j^-)}{s_{in} - s_j^-} \quad \text{with } s_j^- = s_{in} - m_j - \frac{v^*_{1_j}}{y_1} - \frac{u^*_{2_j}}{y_2} \quad (i = 1, 2) \tag{12}$$

then, for any initial condition in the interior of $\mathbb{R}^3_+$, *the critical point* (s^*, x_1^*, x_2^*) *is a globally asymptotically stable solution of system* (8).

In the proof of Theorem 1 we will see that the asymptotic behavior of system (8) can be sketched using lower dimensional (planar) systems: in section 4 we will find some estimations for the substrate $s(t)$ that are dependent of $x_1(t)$ and $x_2(t)$. Using the monotony of f_i, we will build two planar Kolmogorov systems that inherit some properties of system (8) and will make possible to prove that, in a finite time, the solutions of system (8) are in a convex, compact set $K \subset int\mathbb{R}^3_+$. In fact, an elementary analysis based on average Lyapunov functions (see for example [11, Ch.12.2]) and planar competitive systems theory (summarized in Appendix for the convenience of the reader) is sufficient to study their boundedness properties. In section 5 we will improve these bounds and build a Lyapunov-like functional defined in a compact set $K_j \subset K$, that will make possible to prove the main result.

4 Preliminary Results

4.1 Dynamical background and dissipativeness

Standard theorems of differential equations imply that solutions of (8) define a semiflow $\phi\colon \mathbb{R}_+ \times \mathbb{R}^3_+ \mapsto \mathbb{R}^3_+$. A set $C \subset \mathbb{R}_+$ is called *positively invariant* and *globally attractive* if $\phi_t C = C$ for any $t \in \mathbb{R}_+$ and there exists $t_1 \geq 0$ such that $\phi_t x_0 \in C$ for any $t \geq t_1$ and $x_0 \in \mathbb{R}^3_+$. Finally, the semiflow ϕ is *dissipative* if there exists a compact set globally attractive.

We will prove that the semiflow related to solutions of (8) is dissipative; in fact, we prove that there exists a compact and convex set $K \in \mathbb{R}^3_+$ globally attractive and positively invariant. The proof of this later result use planar competitive dynamical systems and average Lyapunov functions. Several results of the next section will be drawn from this result.

4.2 A priori estimates

We introduce the constant θ^* defined by:

$$\theta^* = \frac{s_{in}}{g(0)}(d_1 + d_2),$$

it is no difficult to verify that Eq.(11) implies that $\theta^* < \varepsilon_0$; hence throughout the rest of this paper we will consider $k_0 = \theta^*$.

Before stating the main result of this section, we need to introduce an useful estimation for $\hat{s}(\alpha, \beta)$ which will be used below in several steps of the proof of our main result:

Lemma 1 *The equations*:

$$h_1(s) = f_1(s - \alpha) - g\big(y_1[s_{in} - s]\big) - d_1 = 0, \tag{13}$$

$$h_2(s) = f_2(s - \beta) - g\big(y_2[s_{in} - s]\big) - d_2 = 0, \tag{14}$$

have one root $\eta(\alpha)$ *and* $\xi(\beta)$ *on the intervals* (α, s_{in}) *and* (β, s_{in}) *respectively. Moreover the following inequality holds*:

$$\beta < \xi(\beta) < \hat{s}(\alpha,\beta) < \eta(\alpha) < s_{in} \quad \text{for any } \alpha,\beta \in (0,\theta^*]. \tag{15}$$

Proof: Notice that by monotony of functions f_i and g, it follows that the functions h_i are strictly increasing and they have at most one positive root. By **(G2)** it follows that $h_1(\hat{s}(\alpha,\beta)) < 0$ and Eq.(5) implies that $h_1(s_{in}) > 0$. Hence, the monotony of h_1 implies that Eq.(13) has one solution $\eta(\alpha) \in (\hat{s}(\alpha,\beta), s_{in})$.

Since $h_2(\beta) < 0$ and **(G2)** implies that $h_2(\hat{s}(\alpha,\beta)) > 0$, we prove as before that Eq.(14) has one solution $\xi(\beta) \in (\beta, \hat{s}(\alpha,\beta))$. □

We turn now to the main result of this section.

Theorem 2 *Under the assumptions of Theorem* (1) *but excluding Eq.*(12) *there exists a positively invariant and globally attractive convex set*:

$$K = \left\{(s,x_1,x_2) \in \mathbb{R}^3_+ : -\theta^* \le s - s_{in} + \frac{x_1}{y_1} + \frac{x_2}{y_2} \le 0, \quad (x_1,x_2) \in B\right\}$$

where $B = [u^*_{1_0}, v^*_{1_0}] \times [v^*_{2_0}, u^*_{2_0}]$ *and the constants* u^*_i *and* v^*_i (*see Eq.10*) *are defined by*:

$$u^*_{1_0} = \frac{y_1\{y_2[s_{in} - \hat{u}_0] - g^{-1}(f_1(\hat{u}_0 - \theta^*) - d_1)\}}{y_2 - y_1},$$

$$u^*_{2_0} = \frac{y_2\{g^{-1}(f_2(\hat{u}_0) - d_2) - y_1[s_{in} - \hat{u}_0]\}}{y_2 - y_1},$$

$$v^*_{1_0} = \frac{y_1\{y_2[s_{in} - \hat{v}_0] - g^{-1}(f_1(\hat{v}_0) - d_1)\}}{y_2 - y_1},$$

$$v^*_{2_0} = \frac{y_2\{g^{-1}(f_2(\hat{v}_0 - \theta^*) - d_2) - y_1[s_{in} - \hat{v}_0]\}}{y_2 - y_1}.$$

Proof: Notice that, by **(G1)**-**(G2)** with $k_0 = \theta^*$, it follows that the constants $u^*_{i_0}$,$v^*_{i_0}$ are well defined. Now, the proof will be divided into two steps:

Step (i) We will prove that the set:

$$\Gamma = \left\{(s,x_1,x_2) \in \mathbb{R}^3_+ : -\theta^* \le s - s_{in} + \frac{x_1}{y_1} + \frac{x_2}{y_2} \le 0\right\}$$

is positively invariant and globally attractive.

Step (ii) We will prove that the set B is positively invariant and globally attractive.

Step (i) Let $(s(t), x_1(t), x_2(t))$ be an arbitrary solution of system (8). We consider the function $V\colon \mathbb{R}_+ \mapsto \mathbb{R}$ defined by:

$$V(t) = s(t) - s_{in} + \frac{x_1(t)}{y_1} + \frac{x_2(t)}{y_2}.$$

Differentiating V, it follows from system (8) that:

$$V'(t) = -g(x_1 + x_2)V(t) - d_1\frac{x_1}{y_1} - d_2\frac{x_2}{y_2}. \tag{16}$$

Consider the sets:

$$\Gamma_0 = \{(s, x_1, x_2) \in \mathbb{R}^3_+ : V \leq 0\} \quad \text{and} \quad \tilde{\Gamma}_0 = \{(s, x_1, x_2) \in \mathbb{R}^3_+ : -\theta^* \leq V\}.$$

It is not difficult to verify that $\Gamma = \Gamma_0 \cap \tilde{\Gamma}_0$, moreover, notice that if $V = 0$ then $V' < 0$ and the set Γ_0 is positively invariant. Now, we will prove that Γ_0 is globally attractive. If $V(0) \leq 0$, we are done. Now, we suppose that $V(0) > 0$, this implies that $V(t) \leq V(0)\exp(-g(0)t)$. Finally, letting $t \to +\infty$ it follows that:

$$\limsup_{t\to+\infty} V(t) \leq 0.$$

Now, there is no loss of generality when considering only initial conditions in the set Γ_0. Since $x_i < y_i s_{in}$, Eq.(16) implies that:

$$V' > -g(0)V - s_{in}(d_1 + d_2). \tag{17}$$

By (17) it follows that $V'(t) > 0$ when $V(t) = -\theta^*$. Hence, $\tilde{\Gamma}_0$ is positively invariant.

We consider also the following differential equation:

$$w' = -g(0)w - s_{in}(d_1 + d_2), \quad w(0) \leq V(0).$$

By the comparison Theorem for differential equations (see for example [10, III.4.1],[23, Th.9.5]), it follows that:

$$w(t) \leq V(t) \quad \text{for any } t \geq 0. \tag{18}$$

Now, we will prove that there exists a number $t_1 > 0$ such that $V(t) \in [-\theta^*, 0]$ for any $t \geq t_1$. Indeed, letting $t \to +\infty$, since $\lim_{t\to+\infty} w(t) = -\theta^*$, it follows from Eq.(18) that:

$$-\theta^* \leq \liminf_{t\to+\infty} V(t)$$

and, in consequence Γ is positively invariant and globally attractive.

Step (ii) We will need the following lemma:

Lemma 2 *The set* $\Lambda = \left\{(s, x_1, x_2) \in \Gamma\colon \frac{x_1}{y_1} + \frac{x_2}{y_2} \leq s_{in} - \theta^*\right\}$ *is positively invariant and globally attractive.*

The proof will be given later, we continue now with the proof of theorem. By Lemma 2 there is no loss of generality in consider only initial conditions in the set Λ, moreover it follows that:

$$s_{in} - \theta^* - \frac{x_1}{y_1} - \frac{x_2}{y_2} \leq s \leq s_{in} - \frac{x_1}{y_1} - \frac{x_2}{y_2}.$$

From these inequalities and Lemma 2, it follows that the solutions of system (8) satisfy the following differential inequalities in the set Λ:

$$\begin{cases} \dot{x}_1 \geq x_1\Big(f_1(s_{in} - \theta^* - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1+x_2) - d_1\Big), \\ \dot{x}_2 \leq x_2\Big(f_2(s_{in} - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1+x_2) - d_2\Big). \end{cases} \tag{19}$$

$$\begin{cases} \dot{x}_1 \leq x_1\Big(f_1(s_{in} - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1+x_2) - d_1\Big), \\ \dot{x}_2 \geq x_2\Big(f_2(s_{in} - \theta^* - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1+x_2) - d_2\Big). \end{cases} \tag{20}$$

In order to study these inequalities, we build the following comparison systems defined in Λ:

$$\begin{cases} \dot{u}_1 = u_1\Big(f_1(s_{in} - \theta^* - \frac{u_1}{y_1} - \frac{u_2}{y_2}) - g(u_1+u_2) - d_1\Big), \\ \dot{u}_2 = u_2\Big(f_2(s_{in} - \frac{u_1}{y_1} - \frac{u_2}{y_2}) - g(u_1+u_2) - d_2\Big), \\ 0 < u_1(0) \leq x_1(0) \quad \text{and} \quad u_2(0) \geq x_2(0) > 0. \end{cases} \tag{21}$$

$$\begin{cases} \dot{v}_1 = v_1\Big(f_1(s_{in} - \frac{v_1}{y_1} - \frac{v_2}{y_2}) - g(v_1+v_2) - d_1\Big), \\ \dot{v}_2 = v_2\Big(f_2(s_{in} - \theta^* - \frac{v_1}{y_1} - \frac{v_2}{y_2}) - g(v_1+v_2) - d_2\Big), \\ v_1(0) \geq x_1(0) > 0 \quad \text{and} \quad 0 < v_2(0) \leq x_2(0). \end{cases} \tag{22}$$

Since f_i and g are increasing, we see that the systems (21) and (22) are *competitive* in Λ (*i.e.* the off–diagonal entries of the Jacobian matrix are negative or zero) and its solutions are bounded. Hence, Proposition (i) of 3 (see Appendix) shows that their solutions are convergent to a critical point.

Taking $(\alpha, \beta) = (\theta^*, 0)$ and $(\alpha, \beta) = (0, \theta^*)$, properties **(F)** and **(G)** combined with a simple algebraic calculation shows that systems (21) and (22) have one interior critical points denoted by $(u_{1_0}^*, u_{2_0}^*)$ and $(v_{1_0}^*, v_{2_0}^*)$ respectively. We will prove that they are global attractors.

Moreover, using Eqs.(13) and (14) with $(\alpha, \beta) = (\theta^*, 0)$ and $(\alpha, \beta) = (0, \theta^*)$ respectively, it follows that system (21) has three critical points in $\Lambda \cap \partial\mathbb{R}_2^+$: $(0,0)$,$(\eta_1, 0)$ and $(0, \eta_2)$ where $\eta_i = s_{in} - \frac{\bar{\eta}_i}{y_i}$ and $\bar{\eta}_i$ $(i = 1, 2)$ are solutions of Eqs.(13) and (14) respectively.

It can be proved that the set $\Lambda \cap \partial\mathbb{R}_2^+$ is not attractive. We will sketch this proof for the solution of system (21):

- We build the functional $P\colon \Lambda \mapsto \mathbb{R}$ defined by $P(u_1, u_2) = u_1 u_2$.
- Notice that $P = 0$ for any value in $\Lambda \cap \partial\mathbb{R}_+^2$ and $P > 0$ for any value in $int\Lambda$.

• It follows from system (21) that, $\dot{P} = \Psi(u_1,u_2)P$, where $\Psi\colon \Lambda \mapsto \mathbb{R}$ is the continuous function:

$$\Psi(u_1,u_2) = f_1\Big(s_{in} - \theta^* - \frac{u_1}{y_1} - \frac{u_2}{y_2}\Big) + f_2\Big(s_{in} - \frac{u_1}{y_1} - \frac{u_2}{y_2}\Big) - 2g(u_1+u_2) - (d_1+d_2).$$

• Eq.(15) implies that $\Psi(\eta_1,0) > 0$ and $\Psi(0,\eta_2) > 0$. Moreover **(G2)** and monotony of f_i and g imply that $f_1(s_{in}-\theta^*) - g(0) > 0$ and consequently $\Psi(0,0) > 0$. This imply that P is an *average Lyapunov function* (see [11, Ch.12.2]) and using a result of Hofbauer (see for example [11, Th.12.2.1]), it follows that any solution $(u_1(t),u_2(t))$ cannot be convergent to $\Lambda \cap \partial\mathbb{R}^2_+$ and following (i) of Proposition 3 must be convergent to $(u^*_{1_0}, u^*_{2_0})$.

We proceed analogously to prove that every solution of (22) is convergent to the interior critical point. Hence, it follows that:

$$\lim_{t\to+\infty}(u_1(t),u_2(t)) = (u_1^*,u_2^*) \quad \text{and} \quad \lim_{t\to+\infty}(v_1(t),v_2(t)) = (v_1^*,v_2^*). \tag{23}$$

Using (ii) and (iii) of Proposition 3 (see Appendix) it follows that:

$$u_1(t) \le x_1(t) \le v_1(t) \quad \text{and} \quad v_2(t) \le x_2(t) \le u_2(t) \quad \text{for any } t \ge 0. \tag{24}$$

Considering Eqs.(21)–(22) with initial conditions $(u_1(0),u_2(0)) = (u^*_{1_0},u^*_{2_0})$ and $(v_1(0),v_2(0)) = (v^*_{1_0},v^*_{2_0})$, and using Eqs.(23)–(24) we conclude that the box B is positively invariant.

Now, we will prove that B is globally attractive. We consider an initial condition for inequalities (19)–(20) such that $(x_1(0),x_2(0)) \notin B$. As above, letting $t \to +\infty$, Eqs.(23)-(24) imply that:

$$u^*_{1_0} \le \liminf_{t\to+\infty} x_1(t) \le \limsup_{t\to+\infty} x_1(t) \le v^*_{1_0} \quad \text{and} \quad v^*_{2_0} \le \liminf_{t\to+\infty} x_2(t) \le \limsup_{t\to+\infty} x_2(t) \le u^*_{2_0}$$

and this completes the proof. □

Remark 2 *Brower's fixed point theorem* (see *e.g.* [3, Th. 3.2],[26, Prop. 2.6]) *implies that there exists one fixed point* $(s^*,x_1^*,x_2^*) \in intK$.

4.3 Proof of Lemma 2

We make the proof under the assumption that $-\theta^* \le V \le 0$. Let $(s(t),x_1(t),x_2(t))$ be an arbitrary solution of system (8); we build the function $h : \mathbb{R}_+ \mapsto \mathbb{R}_+$ defined by:

$$h(t) = \frac{x_1(t)}{y_1} + \frac{x_2(t)}{y_2}.$$

(i) First, we will prove that if there exists $t_0 \ge 0$ such that $h(t_0) = s_{in} - \theta^*$ then $h'(t_0) < 0$ that implies positive invariance.

By $h(t_0) = s_{in} - \theta^*$ and $V < 0$, is straightforward to verify that $s(t_0) < \theta^*$. Moreover, differentiating $h(t)$, it follows from system (8) that:

$$h'(t_0) \le h(t_0)\Big(f_{\max}(\theta^*) - g(x_1+x_2) - d_{\min}\Big).$$

If $f_{\max}(\theta^*) \leq d_{\min}$, we are done. Now, suppose that $f_{\max}(\theta^*) > d_{\min}$, since $x_1 + x_2$ is a linear function in the plane $h(t_0) = s_{in} - \theta^*$, it follows that:

$$\min_{(x_1,x_2):h(t_0)=s_{in}-\theta^*} \{x_1 + x_2\} = y_2(s_{in} - \theta^*).$$

Combining these two estimates with the monotony of g, we obtain:

$$h'(t_0) \leq h(t_0)\Big(f_{\max}(\theta^*) - g(y_2[s_{in} - \theta^*]) - d_{\min}\Big).$$

By Eq.(5), it follows that $f_i(\theta^*) < g(0) < g(y_2[s_{in} - \theta^*]) + d_{\min}$ for any $i = 1, 2$, hence $h'(t_0) < 0$.

(ii) We will prove that there exists $t_1 > 0$ such that $h(t_1) = s_{in} - \theta^*$ and $h(t) < s_{in} - \theta^*$ for any $t > t_1$, that implies global attractivity.

Indeed, otherwise we would have $h(t) > s_{in} - \theta^*$ for any $t \geq 0$; as above, it is not difficult to verify that $s(t) < \theta^*$ for any $t \geq 0$; thus:

$$h'(t) \leq h(t)\big(f_{\max}(\theta^*) - g(x_1(t) + x_2(t)) - d_{\min}\big) \quad \text{for any } t \geq 0.$$

Moreover, the solutions of system (8) are defined in the convex set:

$$\Theta = \Big\{(s, x_1, x_2) \in \Gamma\colon \big(s_{in} - \theta^*\big) \leq \frac{x_1}{y_1} + \frac{x_2}{y_2} \leq s_{in}\Big\}.$$

Since $x_1 + x_2$ is a linear function in Θ, it follows that:

$$\min_{(x_1,x_2)\in\Theta} \{x_1 + x_2\} = y_2(s_{in} - \theta^*).$$

This implies that $g(x_1(t) + x_2(t)) > g(y_2[s_{in} - \theta^*])$ for any $t \geq 0$ and by Eqs.(6)–(8) it follows that:

$$x_i'(t) \leq x_i(t)\Big(f_{\max}(\theta^*) - g(y_2[s_{in} - \theta^*]) - d_{\min}\Big) < 0 \quad (i = 1, 2)$$

Notice that $\lim_{t\to+\infty} x_i(t)$ exists and $x_i'(t)$ is uniformly continuous in $[0, +\infty)$. A result of Barbălat (see [6, Lemma 1.2.3]) implies that $\lim_{t\to+\infty} x_i'(t) = 0$ for $i = 1, 2$.

To finish the proof we prove that the solutions $x_i(t)$ can not be convergent to 0. Hence, we must rule out two possible cases: the washout of biomass from the chemostat and the existence of only one $i \in \{1, 2\}$ such that $x_i(t)$ is convergent to 0.

By Eq.(5) we have that the critical point $(s_{in}, 0, 0)$ is a repeller and consequently, the washout of the biomass can not be possible; hence, without loss of generality, we rule out the following type of asymptotic behavior:

$$\lim_{t\to+\infty} (x_1(t), x_2(t)) = (c, 0) \quad (c > 0),$$

indeed, otherwise this implies that

$$\lim_{t\to+\infty}\frac{x_1'(t)}{x_1(t)} = \lim_{t\to+\infty} f_1(s(t)) - g(x_1(t)+x_2(t)) - d_1 = 0$$

as $s(t)\leq\theta^*$, it follows that:

$$\lim_{t\to+\infty}\frac{x_1'(t)}{x_1(t)} = 0 \leq \lim_{t\to+\infty} f_1(\theta^*) - g(x_1(t)+x_2(t)) - d_1.$$

Letting $t\to+\infty$ we have that $f_1(\theta^*)\geq g(c)+d_1 > g(0)+d_1$, obtaining a contradiction with Eq.(5); hence $x_i(t)$ cannot be convergent to 0.

Finally, as $x_i(t)$ is convergent to a positive critical point of system (8) for $i=1,2$ it follows that:

$$\lim_{t\to+\infty} f_1(s(t)) - f_2(s(t)) - d_1 + d_2 = 0$$

and **(F3)** implies that $s(t)$ must be convergent to w^* or s^*; notice that $s(t)$ cannot be convergent to w^* because this implies that there exists a critical point of type $(w^*, x_1(w^*), x_2(w^*))$. Now, if $s(t)$ is convergent to s^* then it follows that $s^*\leq\theta^*$, which is not possible by the left inequality of (5). □

5 Proof of main result

Throughout this section, it is assumed that the initial conditions are in K. We have divided the proof in a sequence of lemmas and the key points of this proof are the generalization of estimations given for the attractor K:

• In Lemma 3 we prove -under the same assumptions as in Theorem 2- that there exists an attractor $K_1\subset K$ for the solutions of Eq.(8). The proof is similar to the proof of Th.2, nevertheless we shall do a sketch of the proof to point out its recursive feature.

• In Lemma 4 we generalize the conclusions of Lemma 3 for a decreasing sequence of attractors $K_j\subset K_1$.

• In Lemma 5, we prove that if there exists an integer $j\in\{1,2,\ldots\}$ such that the inequalities:

$$d_i < \frac{M_j f_i(s_j^-)}{s_{in}-s_j^-}, \quad i=1,2$$

are verified, then any solution in the set K_j is convergent to the critical point (s^*, x_1^*, x_2^*). The main tool is a Lyapunov–like functional $W: K_j\mapsto\mathbb{R}$.

Lemma 3 *Under the assumptions and conditions of Theorem* 2*, there exists a positively invariant and globally attractive set* $K_1\subset K$ *defined by*:

$$K_1 = \Big\{(s,x_1,x_2)\in K\colon -m_1\leq V\leq -M_1 \quad \text{and} \quad (x_1,x_2)\in B_1\Big\}$$

where $B_1=[u_{1_1}^*, v_{1_1}^*]\times[v_{2_1}^*, u_{2_1}^*]$ *and the constants* $u_{1_1}^*$,$u_{2_1}^*$,$v_{1_1}^*$ *and* $v_{2_1}^*$ *are defined in* (10).

Proof: Following the lines of the proof of Theorem 1, it may be concluded that the set $\Gamma_1 = \Big\{(s, x_1, x_2) \in K\colon -m_1 \leq V \leq -M_1\Big\}$ is positively invariant and globally attractive.For convenience of the reader, we will sketch the main lines of the proof.

Differentiating the functional V with respect to t and using the estimations for x_1 and x_2 given by Theorem 1, it follows that:

$$V' > -g(u^*_{1_0} + v^*_{2_0})V - d_1\frac{v^*_{1_0}}{y_1} - d_2\frac{u^*_{2_0}}{y_2}, \tag{25}$$

$$V' < -g(v^*_{1_0} + u^*_{2_0})V - d_1\frac{u^*_{1_0}}{y_1} - d_2\frac{v^*_{2_0}}{y_2}. \tag{26}$$

We consider the following differential equations:

$$w' = -g(u^*_{1_0} + v^*_{2_0})w - d_1\frac{v^*_{1_0}}{y_1} - d_2\frac{u^*_{2_0}}{y_2}, \quad w(0) \leq V(0),$$

$$z' = -g(v^*_{1_0} + u^*_{2_0})z - d_1\frac{u^*_{1_0}}{y_1} - d_2\frac{v^*_{2_0}}{y_2}, \quad z(0) \geq V(0).$$

By the comparison Theorem for differential equations (see *e.g.*[10, III.4.1],[23, Th.9.5]), it follows that:

$$w(t) \leq V(t) \leq z(t) \quad \text{for any } t \geq 0. \tag{27}$$

By Eqs.(25)-(26), it follows that $V'(t) > 0$ ($V'(t) < 0$) when $V(t) = -m_1$ ($V(t) = -M_1$). Hence, Γ_1 is positively invariant.

Let us recall that:

$$m_1 = \frac{\frac{d_1}{y_1}v^*_{1_0} + \frac{d_2}{y_2}u^*_{2_0}}{g(u^*_{1_0} + v^*_{2_0})} \quad \text{and} \quad M_1 = \frac{\frac{d_1}{y_1}u^*_{1_0} + \frac{d_2}{y_2}v^*_{2_0}}{g(v^*_{1_0} + u^*_{2_0})}.$$

Letting $t \to +\infty$, Eq.(27) implies:

$$-m_1 \leq \liminf_{t\to+\infty} V(t) \leq \limsup_{t\to+\infty} V(t) \leq -M_1,$$

hence Γ_1 is globally attractive.

An immediate consequence are the inequalities $0 < M_1 < m_1 < \theta^*$. In the rest of the proof we will suppose that the initial conditions are in Γ_1, hence we have the inequalities:

$$s_{in} - m_1 - \frac{x_1}{y_1} - \frac{x_2}{y_2} \leq s \leq s_{in} - M_1 - \frac{x_1}{y_1} - \frac{x_2}{y_2}.$$

Let us define the set $\Lambda_1 = \Big\{(s, x_1, x_2) \in \Gamma_1\colon \frac{x_1}{y_1} + \frac{x_2}{y_2} \leq s_{in} - m_1\Big\}$, by the inequality $m_1 < \theta^*$, it follows that $\Lambda \subset \Lambda_1$. Hence, Lemma 2 implies that the set Λ_1 is positively invariant and globally attractive and that the solutions of system (8) satisfy the following differential inequalities in Λ_1:

$$\begin{cases} \dot{x}_1 \geq x_1\Big(f_1(s_{in} - m_1 - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1 + x_2) - d_1\Big), \\ \dot{x}_2 \leq x_2\Big(f_2(s_{in} - M_1 - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1 + x_2) - d_2\Big). \end{cases} \tag{28}$$

$$\begin{cases} \dot{x}_1 \leq x_1\Big(f_1(s_{in} - M_1 - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1 + x_2) - d_1\Big), \\ \dot{x}_2 \geq x_2\Big(f_2(s_{in} - m_1 - \frac{x_1}{y_1} - \frac{x_2}{y_2}) - g(x_1 + x_2) - d_2\Big). \end{cases} \tag{29}$$

We consider also the comparison systems defined in Λ_1:

$$\begin{cases} \dot{u}_1 = u_1\Big(f_1(s_{in} - m_1 - \frac{u_1}{y_1} - \frac{u_2}{y_2}) - g(u_1 + u_2) - d_1\Big), \\ \dot{u}_2 = u_2\Big(f_2(s_{in} - M_1 - \frac{u_1}{y_1} - \frac{u_2}{y_2}) - g(u_1 + u_2) - d_2\Big), \\ 0 < u_1(0) \leq x_1(0) \quad \text{and} \quad u_2(0) \geq x_2(0) > 0. \end{cases} \tag{30}$$

$$\begin{cases} \dot{v}_1 = v_1\Big(f_1(s_{in} - M_1 - \frac{v_1}{y_1} - \frac{v_2}{y_2}) - g(v_1 + v_2) - d_1\Big), \\ \dot{v}_2 = v_2\Big(f_2(s_{in} - m_1 - \frac{v_1}{y_1} - \frac{v_2}{y_2}) - g(v_1 + v_2) - d_2\Big), \\ v_1(0) \geq x_1(0) > 0 \quad \text{and} \quad 0 < v_2(0) \leq x_2(0). \end{cases} \tag{31}$$

Let (u_{1_1}, u_{2_1}) and (v_{1_1}, v_{1_2}) be the solutions of the competitive systems (30) and (31) respectively. Following the lines of the proof of Theorem 2, Proposition 3 implies:

$$u_{1_1}(t) \leq x_1(t) \leq v_{1_1}(t) \quad \text{and} \quad v_{2_1}(t) \leq x_2(t) \leq u_{2_1}(t) \quad \text{for any } t \geq 0. \tag{32}$$

As in the proof of Theorem 2, using the same average Lyapunov function $P(u_1, u_2)$, we can conclude that:

$$\lim_{t \to +\infty} (u_{1_1}(t), u_{2_1}(t)) = (u^*_{1_1}, u^*_{2_1}) \quad \text{and} \quad \lim_{t \to +\infty} (v_{1_1}(t), v_{2_1}(t)) = (v^*_{1_1}, v^*_{2_1}). \tag{33}$$

Putting $(u_1(0), u_2(0)) = (u^*_{1_1}, u^*_{2_1})$, $(v_1(0), v_2(0)) = (v^*_{1_1}, v^*_{2_1})$ and using Proposition 3 and Eqs.(32)–(33), we conclude that the box B_1 is positively invariant. Now, if we suppose that $(x_1(0), x_2(0)) \notin B_1$, as in the proof of Theorem 2 we prove that B_1 is globally attractive. $\square$

Let us emphasize that we can proceed recursively to improve the bounds and obtain a decreasing sequence of positively invariants and globally attractive sets K_i, this is the statement of the following lemma:

Lemma 4 *Under the assumptions and conditions of Theorem 2, there exists a decreasing sequence $K_j \subset K_{j-1} \subset \ldots \subset K_1$ of positively invariant and globally attractive sets defined by*:

$$K_j = \Big\{(s, x_1, x_2) \in K_{j-1} \colon -m_j \leq V \leq -M_j \quad \text{and} \quad (x_1, x_2) \in B_j\Big\}.$$

The sets B_j $(j = 2, 3, \ldots)$ *are defined by:*

$$B_j = [u^*_{1_j}, u^*_{2_j}] \times [v^*_{1_j}, v^*_{2_j}],$$

and the constants m_j *and* M_j *are defined by:*

$$m_j = \frac{\left[\frac{d_1}{y_1} v^*_{1_{j-1}} + \frac{d_2}{y_2} u^*_{2_{j-1}}\right]}{g(u^*_{1_{j-1}} + v^*_{2_{j-1}})} \quad \text{and} \quad M_j = \frac{\left[\frac{d_1}{y_1} u^*_{1_{j-1}} + \frac{d_2}{y_2} v^*_{2_{j-1}}\right]}{g(v^*_{1_{j-1}} + u^*_{2_{j-1}})}$$

where the numbers $u^*_{1_j}$,$u^*_{2_j}$,$v^*_{1_j}$ *and* $v^*_{2_j}$ *are defined by Eqs.*(9) *and* (10).

Proof: The proof is similar to the proof of Lemma 3. □

Remark 3 *An immediate consequence of Lemmas* 3 *and* 4 *is that the sequences* $\{M_j\}$,$\{u^*_{1_j}\}$ *and* $\{v^*_{2_j}\}$ *are monotone increasing; the sequences* $\{m_j\}$,$\{v^*_{1_j}\}$ *and* $\{u^*_{2_j}\}$ *are monotone decreasing; moreover the following inequalities are verified for any integer* $j \in \{0, 1, \ldots\}$:

$$M_j < m_j, \quad u^*_{1_j} < v^*_{1_j} \quad \text{and} \quad v^*_{2_j} < u^*_{2_j}.$$

Lemma 5 *Under the same assumptions of Theorem* 2 *and moreover if there exists an integer* $j \in \{1, 2, \ldots\}$ *such that the following inequalities hold for* $i = 1, 2$:

$$d_i \leq \frac{1}{\mu} \frac{f_i(s_j^-)}{s_{in} - s_j^-}, \quad \text{with} \quad \mu \geq 1/M_j \quad \text{and} \quad s_j^- = \min\{s \in K_j\} \tag{34}$$

then the critical point (s^*, x^*_1, x^*_2) *is a globally asymptotically stable solution of system* (8).

Proof: We build the following Lyapunov–like functionals $W_\mu : K_j \mapsto \mathbb{R}$:

$$W_\mu = \int_{s^*}^{s} \frac{d\xi}{s_{in} - \xi} - \mu\Big(s - s^* + \sum_{i=1}^{2} \frac{x_i - x^*_i}{y_i}\Big) \quad \text{for any } \mu > 0. \tag{35}$$

It is clear that:

$$\dot{W}_\mu = g(x_1 + x_2)\Big(1 + \mu V\Big) + \sum_{i=1}^{2} \frac{x_i}{y_i}\Big(\mu d_i - \frac{f_i(s)}{s_{in} - s}\Big).$$

The following properties are elementary:

(i) W_μ and $\dot{W}_\mu$ are continuous and bounded in $[0, +\infty)$.

(ii) By inequality (34) and the bounds for V given by Lemma 4, it follows that $\dot{W}_\mu \leq 0$ for any $\mu \geq \frac{1}{M_j}$.

(iii) As $\lim_{t\to+\infty} W_\mu(t)$ exists and $\dot{W}_\mu(t)$ is uniformly continuous in $[0,+\infty)$, a result of Barbălat (see [6, Lemma 1.2.3]) implies that:

$$\lim_{t\to+\infty} \dot{W}_\mu(t) = 0 \quad \text{for any } \mu \geq \tfrac{1}{M_j}.$$

Define

$$E = \Big\{(s,x_1,x_2) \in \bar{K}_j \colon \dot{W}_\mu = 0\Big\}.$$

Let $\mathcal{M}$ be the union of all invariant solutions in E. Notice that $(s^*,x_1^*,x_2^*) \in \mathcal{M}$, by LaSalle invariance principle, it follows that $\lim_{t\to+\infty} \big(s(t),x_1(t),x_2(t)\big) \in \mathcal{M}$.

We will prove that $(s^*,x_1^*,x_2^*) = \mathcal{M}$. Firstly, we need to improve the characterisation of the sets E and $\mathcal{M}$, for this task we build the sets

$$E_1 = \Big\{(s,x_1,x_2) \in \bar{K}_j \colon \dot{W}_1 = 0\Big\} \quad \text{and} \quad E_2 = \Big\{(s,x_1,x_2) \in \bar{K}_j \colon \dot{W}_2 = 0\Big\}.$$

We shall prove that $E = E_1 \cup E_2$. Firstly, we suppose that $(s,x_1,x_2) \in E_1 \cup E_2$, notice that the relation $\dot{W}_\mu = \dot{W}_1 - \mu \dot{W}_2$ implies that $E_1 \cup E_2 \subseteq E$. Now, to prove the opposite relation we suppose that $(s,x_1,x_2) \in E$. It follows immediately that for any couple of numbers $\lambda, \mu \geq \frac{1}{M_j}$ it follows that:

$$\lim_{t\to+\infty} \dot{W}_\lambda(t) - \dot{W}_\mu(t) = (\mu - \lambda) \lim_{t\to+\infty} \dot{W}_2 = 0$$

and this implies that $(s,x_1,x_2) \in E_2$. Combining this result with the property (iii) of the functional W_μ stated before, we have that $\lim_{t\to+\infty} \dot{W}_1 = 0$, hence $E \subseteq E_1 \cup E_2$ and consequently $E = E_1 \cup E_2$.

As a direct consequence of this equality, we have two characterizations for the set E

$$E = \Big\{(s,x_1,x_2) \in \bar{K}_j \colon F_1(s,x_1,x_2) = F_2(s,x_1,x_2) = 0\Big\},$$

$$E = \Big\{(s,x_1,x_2) \in \bar{K}_j \colon F_1(s,x_1,x_2) = \tilde{F}_2(s,x_1,x_2) = 0\Big\}$$

where F_1,F_2 and $\tilde{F}_2$ are defined by:

- $F_1(s,x_1,x_2) = \sum\limits_{i=1}^{2} \frac{x_i}{y_i}[g(x_1+x_2) - f_i(s)] - g(x_1+x_2)V,$
- $F_2(s,x_1,x_2) = -g(x_1+x_2)V - \sum\limits_{i=1}^{2} \frac{x_i}{y_i} d_i.$
- $\tilde{F}_2(s,x_1,x_2) = \sum\limits_{i=1}^{2} \frac{x_i}{y_i}[f_i(s) - g(x_1+x_2) - d_i].$

Notice that by equation $F_2(s,x_1,x_2)=0$ and implicit function theorem applied to equation $F_1(s,x_1,x_2)=0$, it can be concluded that E is a union of curves and points defined by the intersection of two surfaces $s_i(x_1,x_2)=0$ $(i=1,2)$, hence the set $\mathcal{M}$ must be a union of the critical point (s^*,x_1^*,x_2^*) with invariant curves in E.

To finish the proof, we will prove that $(s^*,x_1^*,x_2^*)=\mathcal{M}$. For this task, let $u_0=\big(s(0),x_1(0),x_2(0)\big)\in\mathcal{M}$ and let $\phi_t u_0$ be the solution of system (8) with initial condition u_0. There are two cases to consider: (i) $s(0)\neq s^*$ and (ii) $s(0)=s^*$.

If $s(0)\neq s^*$ (without loss of generality we assume that $s(0)<s^*$), the invariance of the orbit implies that

$$F_1(\phi_t u_0)=g(x_1+x_2)(s_{in}-s)-\sum_{i=1}^{2}\tfrac{x_i}{y_i}f_i(s)=0,$$

$$\tilde{F}_2(\phi_t u_0)=\textstyle\sum_{i=1}^{2}\tfrac{x_i}{y_i}\underbrace{[f_i(s)-g(x_1+x_2)-d_i]}_{=\lambda(s,x_1,x_2)}$$

for any $t\geq 0$, hence $F_1(s,x_1,x_2)=0$ implies that $s'(t)=0$ and consequently $s(t)=s(0)$ for any $t\geq 0$. Moreover $\tilde{F}_2(s,x_1,x_2)=0$ implies that $\lambda_1(s,x_1,x_2)>0>\lambda_2(s,x_1,x_2)$, hence x_1 and x_2 are an increasing and a decreasing function respectively. This monotonicity of functions x_i combined with Lemma 4 imply that there exists a critical point $\tilde{E}\neq(s^*,x_1^*,x_2^*)$ such that $\lim_{t\to+\infty}\phi_t u_0=\tilde{E}$ obtaining a contradiction with the uniqueness of (s^*,x_1^*,x_2^*).

If $s(0)=s^*$, it can be proved that $u_0=(s^*,x_1^*,x_2^*)$, indeed, the invariance of $\mathcal{M}$ combined with **(F3)** imply that $\big(x_1(0),x_2(0)\big)$ is a solution of the equations

$$F_1(u_0)=g(x_1+x_2)(s_{in}-s^*)-\sum_{i=1}^{2}\frac{x_i}{y_i}f_i(s^*)=0,$$

$$\tilde{F}_2(u_0)=[f_1(s^*)-d_1-g(x_1+x_2)]\underbrace{\sum_{i=1}^{2}\frac{x_i}{y_i}}_{>0}=0$$

and it is an easy exercise to show that $(x_1(0),x_2(0))=(x_1^*,x_2^*)$ and the lemma follows.

We can rewrite $\dot{W}_\mu$ as $\dot{W}_\mu=\dot{W}_1-\mu\dot{W}_2$, where:

$$\dot{W}_1=\frac{\dot{s}}{s_{in}-s}=\frac{1}{s_{in}-s}\Big(\sum_{i=1}^{2}\frac{x_i}{y_i}[g(x_1+x_2)-f_i(s)]-g(x_1+x_2)V\Big),$$

$$\dot{W}_2=-g(x_1+x_2)V-\sum_{i=1}^{2}\frac{x_i}{y_i}d_i.$$

Note that for any couple of numbers $\lambda,\mu\geq\frac{1}{M_j}$ it follows that:

$$\lim_{t\to+\infty}\dot{W}_\lambda(t)-\dot{W}_\mu(t)=(\mu-\lambda)\lim_{t\to+\infty}\dot{W}_2=0$$

and this implies that $\lim_{t\to+\infty} \dot{W}_1(t) = 0$.

As the only solution of equations $\dot{W}_1 = \dot{W}_2 = 0$ is the point (s^*, x_1^*, x_2^*), LaSalle invariance principle implies that:

$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (s^*, x_1^*, x_2^*)$$

and the lemma follows.□

The end of the proof of Theorem 1 is now clear, notice that Lemma 5 gives a sufficient condition for global asymptotic stability expressed in terms of an upper bound of mortality rate d_i. Secondly, it is straightforward to verify that:

$$s_j^- = s_{in} - m_j - \frac{v_{1_j}^*}{y_1} - \frac{u_{2_j}^*}{y_2}.$$

Finally, taking $\mu = 1/M_j$, Eq.(34) is equivalent to Eq.(12) and the Theorem is proved.

6 discussion

In this paper we consider the model of competition in the chemostat –with two species and a single growth limiting substrate– as a control system, choosing the total biomass as the only output available and the dilution rate as the feedback control variable. We built a feedback control law, and Theorem 1 gives some sufficient conditions –summarized as upper bounds for d_i– that ensure (s^*, x_1^*, x_2^*) to be a critical point globally asymptotically stable. This result contrasts with the model without control defined by Eq.(1) in the sense that control makes possible the coexistence between the two species.

Our result extends that of [5] in the way that it deals with bounded mortality rates relaxing the assumption $d_i = 0$. This implies that the asymptotic behavior of the model can not be reduced to a two–dimensional system and therefore we must study the full system.

Despite this improvement, the bounds for mortality rates given by Eqs.(11)–(12) are not optimal and this fact lead us the question about the largest possible bound for d_i to avoid the competitive exclusion.

Several very important issues and possibilities were left out of the present paper. One possibility is the robustness. We wish to obtain the stability of a box $\tilde{K} \in int\mathbb{R}_+^3$ under error in the measurements and uncertainty in identification of growth functions f_i. This case can be solved by the same methods combined with alternative and more technical hypotheses.

Moreover, numerical simulations for the model studied in [7] suggest that this result can be extended to competition models with more general (nonmonotone) uptake functions. This however remains a unsolved problem, as our analysis makes essential use of monotony of f_i. We still do not know how to establish a similar resultby the methods of the present paper.

Still another natural extension of our results would be to treat the case of delayed outputs $y(t) = x_1(t-\tau)+x_2(t-\tau)$ (with $\tau > 0$). In spite of the fact that delays in the measurements are generally small with respect to biological processes and consequently, they could have not impact on the stability of (s^*, x_1^*, x_2^*) (this idea is summarized as *small delays are harmless* [6],[20]), it would be extremely desirable to confirm these ideas by mathematical proofs.

Appendix: Planar competitive systems We review some basic results of competitive dynamical systems theory. We refer to [20],[21] for further details and generalizations as well as for some of the terminology that we use here.

Denote by $K_{(0,1)}$ the convex cone defined by:

$$K_{(0,1)} = \{(u_1, u_2) \in \mathbb{R}^2 : u_1 \geq 0 \quad \text{and} \quad u_2 \leq 0\}$$

and define an order in $\mathbb{R}^2$ by $\vec{y} \leq_{K_{(0,1)}} \vec{x}$ if $\vec{x} - \vec{y} \in K_{(0,1)}$, that means that $y_1 \leq x_1$ and $y_2 \geq x_2$.

Let $F\colon \Omega \mapsto \mathbb{R}^2$ be a continuous function where Ω is an open set in $\mathbb{R}^2$. $F = (F_1, F_2)$ is said to be of type $K_{(0,1)}$ if for each i, $(-1)^{m_i} F_i(\vec{a}) < (-1)^{m_i} F_i(\vec{b})$ for any two points $\vec{a}$ and $\vec{b}$ in Ω satisfying $\vec{a} \leq_{K_{(0,1)}} \vec{b}$, $(m_1, m_2) = (0, 1)$ and $a_i = b_i$.

Note that, if system (36) is competitive and Ω is convex, then F is of type $K_{(0,1)}$.

The goal is to compare solutions of the system of differential equations:

$$\dot{x} = F(x). \tag{36}$$

with solutions of the systems of differential equations:

$$\dot{z} = G(z), \tag{37}$$

$$\dot{y} = H(y). \tag{38}$$

Such that the continuous functions G,$H\colon \Omega \mapsto \mathbb{R}^2$ verify $H \leq_{K_{(0,1)}} F \leq_{K_{(0,1)}} G$.

Proposition 3 (Comparison Theorem) *Let F be continuous on Ω and of type $K_{(0,1)}$. Let $x(t)$ be a maximal solution of* (36) *defined on $[a, b]$, hence*:

(i) If the orbit of each initial condition of (36) *is bounded then $b = +\infty$ and every solution of* (36) *is convergent to a critical point.*

(ii) If $z(t)$ is a continuous function on $[a, b]$ satisfying (37) *on (a, b) with $z(a) \leq_{K_{(0,1)}} x(a)$, then $z(t) \leq_{K_{(0,1)}} x(t)$ for all t in $[a, b]$.*

(iii) If $y(t)$ is a continuous function on $[a, b]$ satisfying (38) *on (a, b) with $y(a) \geq_{K_{(0,1)}} x(a)$, then $y(t) \geq_{K_{(0,1)}} x(t)$ for all t in $[a, b]$.*

Proof: See Lemma 2 from [21] and Theorem 3.2.2 from [20]. □

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